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Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania

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ABSTRACT. A total of 200 variable-area plots covering 20.3 ha containing 4000 trees with a basal area of 921.4 m^2 were assessed over a combined elevational range of 410–2180 m in the moist forests of three Tanzanian Eastern Arc mountains: West Usambara, Nguru and Udzungwa. Plot data were ordinated on the basis of species presence/absence, frequency and basal area. Axis 1 of ordinations based on species presence/absence are correlated with elevation. Axis 1 of the frequency-weighted ordination was correlated with elevation in the Nguru and Udzungwa mountains, but plots from the West Usambara showed a rainfall-related discontinuity. Axis 1 of the West Usambara basal area-weighted ordination showed evidence of long-term dynamics of *Ocotea usambarensis* and in the Udzungwa mountains was determined by presence of *Parinari excelsa*. Plot diversity was not correlated with elevation or latitude, but was lower in disturbed, low rainfall or more seasonal forest. Stem density was positively correlated with elevation and was greater on ridge tops than valley sides and valley bottoms.

KEY WORDS: diversity, elevational variation, ordination, structure, tropical forest, Tanzania.

INTRODUCTION

A number of studies suggest that there are zones or belts of vegetation on tropical mountains in which there is elevation-related discontinuous variation in floristic composition or structure. In a review of the vegetation of East African high mountains, Hedberg (1951) identified three main vegetation belts: the montane forest belt, the ericaceous belt and the alpine belt. The montane forest belt could be divided into three zones, the montane forest zone, the bamboo zone and the *Hagenia–Hypericum* zone. A phytogeographical division in eastern African forests between an upper Afromontane and lower Zanzibar–Inhambane region was recognized by White (1983a). The upper elevation limit of the Zanzibar–Inhambane region was considered to be generally below 200 m in elevation, but reaching 1254 m in the East Usambara mountains. In Malesia

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a study of elevational ranges of the mountain flora showed discontinuities at elevations of 1000, 1500, 2400 and 3400–4000 m (van Steenis 1984). Similarly, a study of Mt Cameroon suggested that there are critical elevations on African forested mountains at 800, 1500, 2300, 3000 and 4500 m (Boughey 1955). In north-east tropical Africa, agglomerative clustering analysis of forest tree elevational distribution, using Jaccard's similarity coefficient based on species presence or absence, gave zonations at 305, 915, 1525, 2745 and 3355 m (Friis 1992). Divisive analysis of the same data set using TWINSPAN gave divisions at 1220, 2440 and 3355 m (Friis & Lawesson 1993).

Other studies have suggested that elevational variation in vegetation can be continuous. In Malawi, submontane seasonal rainforest occurring above 1370 m was observed to be similar in structure, physiognomy and taxonomic relationships to lowland seasonal rainforest; and there is not a clear-cut elevational separation between montane and submontane forest (Chapman & White 1970). In Uganda, a study of elevational variation of forest trees using Jaccard's similarity coefficient, without using cluster analysis, for elevations between 1219 and 3353 m suggested that there was an elevational continuum (Hamilton 1975). In the East Usambara mountains of Tanzania, variation in axis 1 of a DECORANA ordination of tree plots based on both species presence/absence and frequency from an altitude of 290 to 1220 m also showed an elevational continuum (Hamilton *et al.* 1989).

In its simplest form, the relationship between elevation and species composition can be represented by a model in which there are two gradients, one from higher elevation and the other from lower elevation. Species adapted to high elevations will become progressively rarer at lower elevations, and vice versa for low elevation adapted species. If samples are then taken from along this environmental continuum, apparent discontinuities will be dependent on the sampling technique and method of analysis. Discontinuous sampling will produce zones corresponding to the chosen sampling limits, and the use of divisive classification methods will divide gradients into upper and lower elevation types which would otherwise be revealed as continuous by ordination methods. However, this two-gradient model does not take into account dynamic processes such as cyclical changes in forest composition related to successional stage, either as a result of stochastic events, or driven by climatic change, geological upheaval or other forms of disturbance. These dynamic processes may account for discontinuous variation in species composition which is then interpreted as evidence for zonation. In complex species-rich vegetation types, such as tropical forests, a simple consideration of species presence or absence may not reveal temporal changes. Ideally data need to be weighted by age of sampled individuals; however, this is difficult to achieve and so more easily measured parameters such as frequency or size must be used as an alternative.

If there is zonation in tropical forests, then this might be reflected in other aspects of communities such as structure and diversity. Species diversity is considered to change with elevation as a function of productivity, with less

diverse communities occurring at higher elevations. Empirical data indicate that this relationship is unimodal, with diversity at first increasing with productivity and then falling (Rosenzweig 1992, Rosenzweig & Abramsky 1993). Similarly, rainfall is related to potential productivity and hence diversity (Wright *et al.* 1993) with a correlation between species richness and rainfall being found in some Neotropical forests (Gentry 1982, 1988, 1989). Temporal factors have also been implicated as determinants of diversity, with history of an area being suggested to account for discrepancies between productivity and species richness (Latham & Ricklefs 1993).

In eastern tropical Africa, rainfall shows both marked seasonal and geographic variation. Near the equator there is a bimodal rainfall pattern with the warmest months being February and March, whereas to the south there is a monomodal rainfall pattern with a correspondingly more marked dry season and the warmest months being November and December (Griffiths 1972, Lovett 1993a, Pócs 1976a). The forested Eastern Arc mountains of south-eastern Kenya and eastern Tanzania, which are defined as the ancient crystalline mountains under the direct climatic influence of the Indian Ocean (Lovett 1990a), have a bimodal rainfall pattern in the north and monomodal pattern in the south. Northern and southern parts of the Eastern Arc mountains are considered to have had a relatively similar long-term geological and climatic history (Lovett 1993a,b). A comparison of elevational changes in forests under bimodal and monomodal rainfall systems provides an opportunity to look for evidence for zonation and assess the relative importance of climatic patterns and history in determining species composition and diversity. In this study of the forests on three mountains in the Eastern Arc range of Tanzania, data from variable area plots assessing large trees are used to investigate variation in community associations, diversity and structure with elevation and rainfall. On the West Usambara mountains, which are under a bimodal rainfall pattern, variation between sites is investigated by comparing plots from seven areas on the same mountain. On the northern Udzungwa mountains, which is under a monomodal rainfall pattern, valley bottom, valley side and ridge-top plots are compared at a single site. Latitudinal comparisons between northern and southern parts of the Eastern Arc are made using subsets of the Usambara and Udzungwa data, together with a third set of plots from the Nguru mountains. The results are discussed in the context of elevational zonation, environmental discontinuities and dynamic processes.

STUDY SITES

The Eastern Arc mountains range from the Makambako gap in the southern Udzungwa of Tanzania (8° 51′ S, 34° 49′ E) to the Taita Hills in Kenya (3° 25′ S, 38° 20′ E) (Figure 1). A total of 200 plots were assessed from three sites in the Eastern Arc, the West Usambara (93 plots), Southern Nguru (29 plots) and Udzungwa mountains (78 plots) with a combined elevational range

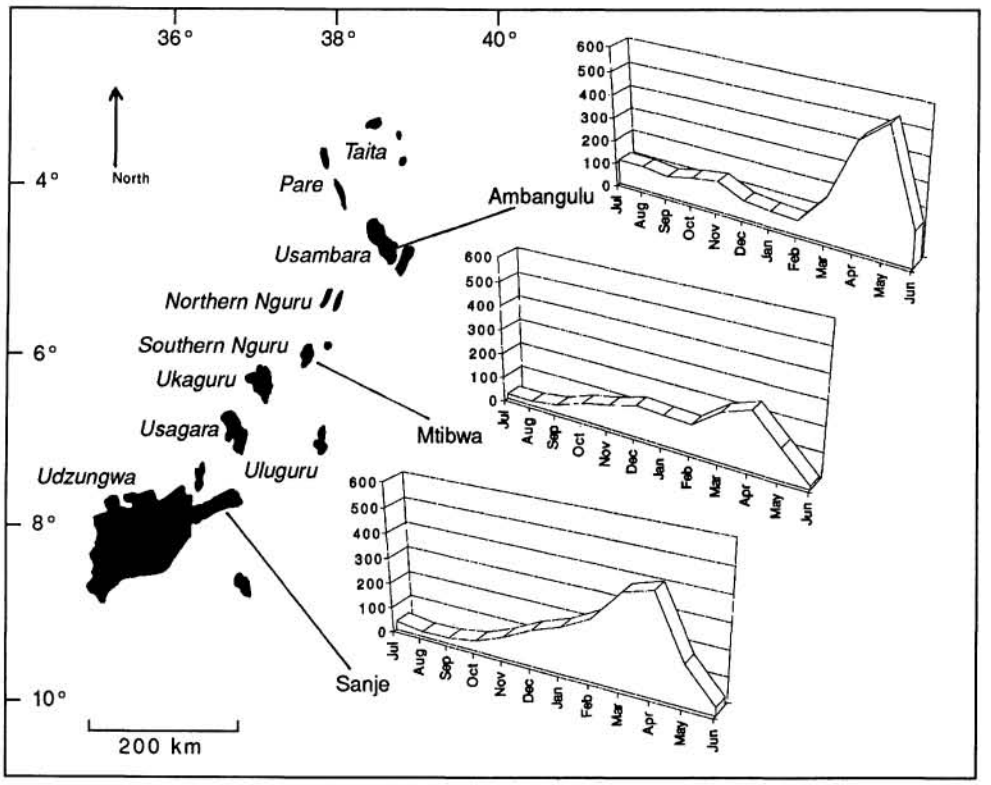

Figure 1. Eastern Arc mountains with monthly rainfall data (mm of rain) for Ambangulu in the West Usambara mountains (5° 4′ S, 38° 25′ E; alt. 1219 m; mean annual rainfall: 2089 mm; years of records: 45); Mtibwa, just east of the southern Nguru mountains (6° 7′ S, 37° 38′ E; alt. 457 m; mean annual rainfall: 1206 mm; years of records: 20); and Sanje at the foot of the Udzungwa mountains (7° 48′ S, 36° 54′ E; alt. 366 m; mean annual rainfall: 1747 mm; years of records: 14). Rainfall on the southern Nguru and Udzungwa mountain forests will be higher than indicated by the rainfall stations, but the pattern will be similar.

of 410–2180 m. The ancient crystalline gneiss rocks of the Eastern Arc are part of the Precambrian Mozambique belt which is composed of highly metamorphosed sediments and minor intrusive igneous bodies (Griffiths 1993). The range originated by block faulting over a long period of time (Griffiths 1993) and earth tremors still occur.

The West Usambara mountains (4° 25′–5° 07′ S, 38° 10′–38° 35′ E) are a large upland block in the northern part of the Eastern Arc range rising to nearly 2300 m and covering *c.* 2200 km^2. The vegetation, flora and geography of the West Usambara have been described by Iversen (1991), Moreau (1935), Pitt-Schenkel (1938) and Rodgers & Homewood (1982a). Specific forest areas are described by Hall (1990), Lovett (1990b, 1991a,b,c,d,e; 1993c,d), Lovett & Pócs (1993) and Lovett & Stuart (in press). The climate of the West Usambara is determined by their position 100 km from the Indian Ocean and less than 5° south of the equator. They have an oceanic climate with a bimodal rainfall peaking in November and April with a mean maximum of 2000 mm of rain a

year in the wettest areas, falling to less than 600 mm on the drier western side. Temperatures in the Usambara mountains are ameliorated by proximity to the sea, and on the East Usambara mountains are lower than those at similar elevations inland (Hamilton 1989, Pócs 1976a). In the West Usambara, moist forest occurs from 150 to 2285 m in elevation and covers extensive areas of the wetter eastern, southern and northern sides of the mountain, with outliers on Mafi Hill to the west and Bumba Mavumbi and Mweni-Gombelo to the east. Of the total forest area of 24,532 ha, less than 2% is below 1065 m (van der Willigen & Lovett 1979). The western side of the mountain is in a rain shadow and so is considerably drier than the eastern side with the vegetation changing accordingly to become woodland, thicket and scrub. The study area covered as many forest areas as possible in an attempt to fully represent elevational and moisture variants of the forest. Areas where forest grows are hilly, but not excessively steep, with rounded ridge tops and valley bottoms. Seven areas were recognized. Ambangulu is the forests at Ambangulu and Kunga on the Ambangulu tea estate in the southern part of the West Usambara (31 plots from 1000 to 1390 m with a rainfall of *c.* 2000 mm y^{-1}). Baga covers the Baga Forest Reserves, Kwagaroto peak and forest on the Herkulu tea estate (17 plots from 1620 to 1950 m with a rainfall of *c.* 1400 mm y^{-1}); Gonja, the Kisima–Gonja Forest Reserve and adjacent forest (5 plots from 1460 to 1650 m with a rainfall of *c.* 1400 mm y^{-1}); and Mkussu, the Mkussu Forest Reserve and adjacent forests near Kifungilo (10 plots from 1510 to 1670 m with a rainfall of *c.* 1000 mm y^{-1}). Shagayu covers the Shagayu Forest Reserve in the northern West Usambara (6 plots from 1850 to 2010 m with a rainfall of *c.* 1000 mm y^{-1}); Shume-*Juniperus*, the remnant of *Juniperus* forest near Shume in the north-western part of the mountains (5 plots from 1840 to 1880 m with a rainfall of 600 to 900 mm y^{-1}); and Shume–Magamba, the Shume–Magamba Forest Reserve, Sungwi peak and adjacent forests at Kwegoma (19 plots from 1760 to 2180 m with a rainfall of *c.* 1100 mm y^{-1}).

The Udzungwa mountains (also spelt Uzungwa, for explanation see Moyer & Lovett, in press) are an extensive upland area formed by fusion of the ancient Mozambique shield of Usagaran biotite gneiss to the south-east and Archaen granites to the north-west, followed by uplift and faulting (Rodgers & Homewood 1982b) in the southern part of the Eastern Arc. They cover about 10,000 km^2 (7° 15′–8° 45′ S, 35° 00′–37° 00′ E) rising from 300 m in the east to peaks of around 2500 m. They are between 300 km in the northern part and 460 km in the southern part from the Indian Ocean. The rainfall is derived from the Indian Ocean and is monomodal with a peak in April. The eastern scarp receives 1800–2000 mm of rain a year and is largely covered in moist forest of which about 450 km^2 remains. Rainfall falls off rapidly to the rain shadow in the west with the vegetation changing to woodland and thicket (Rodgers & Homewood 1982b). The study area was in Mwanihana Forest Reserve, now part of the Udzungwa National Park, in the northern part of the Udzungwa mountains on the steep east-facing escarpment above Sanje village

(7° 50′ S, 36° 55′ E). At Mwanihana there is a continuous elevational range of moist forest from 450–1760 m. Mean annual rainfall at foot of the escarpment on the Sanje Sugar Estate is 1747 mm (elevation 366 m; 14 y of records). Rainfall on the escarpment slopes is probably higher, in the range of 2000–2500 mm y^{-1}. The wet season is from November to May when, on average, greater than 100 mm of rain is received each month. The four-month dry season lasts from July to October when each month receives less than 50 mm of rain on average, and months with no rain are frequent. The escarpment is dissected by steep-sided valleys separated by sharp, exposed ridge tops. Some of the valley bottoms are flat, though nowhere particularly broad. All the plots assessed were within the Sanje river catchment. The vegetation has been described qualitatively (Lovett & Pócs 1993, Lovett & Thomas 1986, Lovett *et al.* 1988) and there have been a number of studies on animals, including birds (Jensen & Brøgger-Jensen 1992), spiders (Scharff 1990) and primates (Wasser 1993).

The Southern Nguru mountains are in the central part of the Eastern Arc (6° 01′–6° 13′ S, 37° 26′–37° 37′ E) and have a monomodal rainfall pattern with a rainy season from November to May, peaking in April. The summit ridge and the eastern slopes of the mountains are covered by a forest reserve north-west of Turiani village with an elevational range of 400–2400 m (Lovett & Pócs 1993, Lovett & Thomas 1988, Pócs *et al.* 1990). The plots were assessed in Nguru South forest in the catchment of the Dikarura river with an elevational range of 880–1560 m.

METHODS

Large tree community associations were assessed using the 20-tree variable-area plotless technique (Hall 1991). The nearest 20 trees of ⩾20 cm dbh to an objectively chosen point were identified and dbh recorded. Distance to the 21st most distant tree was also measured. Species frequency was defined as the number of trees out of 20 in each plot. Although an absolute measurement of plot area was not possible with this method, a relative estimate could be made by considering the plot radius to be half-way between the 21st tree and the 20th tree to provide comparative structural data on basal area and stem density.

The plots were located at 100 m intervals on a compass bearing from an objectively chosen point within a forest area. Lines of plots were positioned to cover as much caternary variation as possible in each locality, from valley bottoms to ridge tops. Plot lines continued until heavily disturbed vegetation or a forest edge was encountered. Field work was carried out with a single field assistant. Measurements of dbh were made with a standard girthing tape. For very large trees or trees with large buttresses, the bole diameter was estimated by measuring the width of the bole above the buttresses. Calculation of basal area was made assuming that the boles are circular. Elevation was measured using an aneroid Thommen altimeter calibrated every day at a known elevation read from 1:50,000 topographic maps.

Trees were identified using slash and bark characters, observation of canopy leaves with binoculars, coppice, low branches or fallen leaves. In addition, names supplied by locally recruited assistants were used as a general guide. When identification was in doubt leaf samples were collected using a catapult or extendible clipper poles. When possible, flowering and fruiting herbarium specimens were made. These were deposited in herbaria at the University of Dar es Salaam (DSM), Royal Botanic Gardens, Kew (K) and Missouri Botanical Garden (MO). Sterile gatherings of unidentified trees were identified at the Royal Botanic Gardens, Kew.

The plot data was analysed using the R-package computer program (Legendre & Legendre 1983, Legendre & Vaudor 1991). Similarity between the plots was calculated for species presence/absence using Jaccard's coefficient of community, species frequency using chi-squared similarity and estimated species basal area using chord distance. In the chi-squared similarity coefficient the commoner species contribute more to similarity between plots than rarer species so plots with dominant species will be emphasized. The chord distance uses a normalized Euclidean distance. Normalization reduces all sample–sample comparisons to proportions of 1.0 and is appropriate for basal area data because total basal area per sample varies greatly, in contrast to total number of individual's per sample, which will always be 20. Data were ordinated using a principal coordinates analysis available in the R-package which has options for both similarity and distance measures. Diversity was calculated by three methods: total number of species in each plot, Simpson's diversity index as a measure of dominance and Shannon's diversity index as a measure of richness (Magurran 1988). Simpson's index is determined more by differences in the representation of the more abundant species and Shannon's more by rare species. Statistical analysis was carried out using *Statview II* (Abacus Concepts 1991) to compute coefficients of determination (r^2) for linear regressions of descriptive variables, and axes scores, or elevation.

RESULTS

In the West Usambara mountains a total of 1860 trees in 93 plots were assessed over an elevational range of 1000–2180 m, covering an estimated 8.7 ha containing 111 species with a total basal area of 463 m^2. In the northern Udzungwa mountains a total of 1560 trees in 78 plots were assessed over an elevational range of 410–1670 m, covering an estimated 9.2 ha containing 169 species with a total basal area of 346 m^2. In the Nguru mountains a total of 580 trees in 29 plots were assessed over an elevational range of 880–1560 m, covering an estimated 2.4 ha containing 62 species with a total basal area of 112.4 m^2. Descriptive statistics of the plots are given in Table 1 and regression statistics of the ordinations in Table 2. The three West Usambara ordinations show marked differences in the relationship between plot elevation and axis 1 and axis 2 value. Plot elevation shows a continuous linear relationship with axis 1

Table 1. Descriptive statistics (a) of plot structural characteristics and diversity in different sites or topographic positions, expressed as means and standard deviations; with regression statistics (b) for each of the three variables against elevation (coefficient of determination and, in parentheses, probability) for the three mountains Usambara, Udzungwa and Nguru in Tanzania.

	Number of plots	Basal area (m^2 ha^{-1})	Stem density (ha^{-1})	Number of species	Simpson index	Shannon index
(a)						
Usambara	93	54.8 ±30.4	238.7 ±81.9	9.2 ±2.2	0.15 ±0.10	1.95 ±0.36
Ambangulu	31	62.7 ±28.7	197.5 ±69.8	9.9 ±1.6	0.12 ±0.06	2.07 ±0.25
Baga	17	65.5 ±36.0	240.9 ±85.5	9.7 ±1.7	0.12 ±0.05	2.04 ±0.24
Gonja	5	38.4 ±11.0	204.2 ±42.5	7.6 ±2.2	0.20 ±0.06	1.69 ±0.27
Mkussu	10	42.5 ±21.2	242.7 ±53.2	8.9 ±2.1	0.14 ±0.06	1.95 ±0.26
Shagayu	6	55.0 ±26.3	305.7 ±56.7	11.2 ±2.0	0.10 ±0.04	2.19 ±0.24
Shume-*Juniperus*	5	17.0 ±5.2	202.8 ±46.8	5.0 ±1.6	0.43 ±0.17	1.10 ±0.36
Shume–Magamba	19	53.3 ±31.1	299.4 ±86.7	8.7 ±2.2	0.16 ±0.11	1.89 ±0.36
Udzungwa	78	42.9 ±25.9	202.1 ±99.4	9.3 ±2.6	0.17 ±0.13	1.92 ±0.42
Ridge top	24	58.2 ±25.4	274.7 ±130.3	8.3 ±2.6	0.20 ±0.16	1.78 ±0.48
Valley bottom	23	38.9 ±26.8	162.0 ±46.4	10.3 ±2.8	0.14 ±0.12	2.03 ±0.43
Valley side	31	34.1 ±20.3	175.8 ±68.1	9.4 ±2.1	0.15 ±0.10	1.94 ±0.35
Nguru	29	48.6 ±26.2	260.0 ±82.0	10.5 ±2.2	0.10 ±0.05	2.14 ±0.26
Ridge top	15	45.1 ±16.1	307.0 ±81.0	11.1 ±2.2	0.09 ±0.04	2.23 ±0.23
Valley side	14	52.3 ±34.1	209.7 ±46.4	9.9 ±2.2	0.12 ±0.05	2.05 ±0.27
(b)						
Usambara	93	0.011	0.258	0.04	0.048	0.047
		(0.31)	(0.0001)	(0.053)	(0.035)	(0.036)
Udzungwa	78	0.303	0.639	0.000	0.01	0.006
		(0.0001)	(0.0001)	(0.94)	(0.39)	(0.48)
Nguru	29	0.048	0.129	0.004	0.066	0.029
		(0.25)	(0.056)	(0.74)	(0.18)	(0.37)

Table 2. Coefficients of determination (r^2) for regressions of elevation against axis 1 and axis 2 scores of the ordinations of forest plots in the Eastern Arc mountains, Tanzania.

	Axis			
	1		2	
	r^2	P	r^2	P
Usambara				
Presence/absence	0.82	***	0.03	ns
Frequency	0.07	*	0.82	***
Basal area	0.57	***	0.30	**
Udzungwa				
Presence/absence	0.66	***	0.03	ns
Frequency	0.87	***	0.24	ns
Basal area	0.02	ns	0.74	***
Nguru				
Presence/absence	0.80	***	0.58	***
Frequency	0.84	***	0.49	***
Basal area	0.24	ns	0.53	***
Mid-elevation				
Presence/absence	0.70	***	0.00	ns
Frequency	0.46	***	0.30	***
Basal area	0.16	***	0.08	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns, not significant.

of the ordination based on species presence/absence. In contrast, there is no relationship between axis 1 of the ordination weighted by frequency and elevation, with the Shume-*Juniperus* plots separated from the other plots, though plot elevation is strongly correlated with axis 2 (Figure 2). Plot elevation is correlated with axis 1 of the ordination weighted by basal area, but not as closely correlated as either axis 1 of the presence/absence or axis 2 of the frequency-weighted ordinations. In particular, two of the Ambangulu plots have high axis 1 values, reducing their distance from higher elevation plots (Figure 3). This is caused by occurrence of four large *Ocotea usambarensis* trees in these two plots. Three species contribute 85% of the basal area in the two plots, *Ocotea* (56%), *Parinari excelsa* (15%) and *Newtonia buchananii* (14%). *Parinari* and *Newtonia* were not recorded above 1550 m in the plots sampled, whereas *Ocotea* was associated with higher elevations. The importance of this observation in relation to the dynamic nature of forest community associations is examined further in the discussion.

Basal area showed a wide variation, with only the Shume-*Juniperus* plots having a significantly lower basal area ($P < 0.01$) in comparison to the plots from the other sites. The Shume-*Juniperus* plots were also significantly less diverse than the other West Usambara plots ($P < 0.01$), though one Shume–Magamba plot dominated by *Macaranga kilimandscharica* was exceptional in the plots from wetter forest in that it had a Simpson's index value of 0.51. Plots

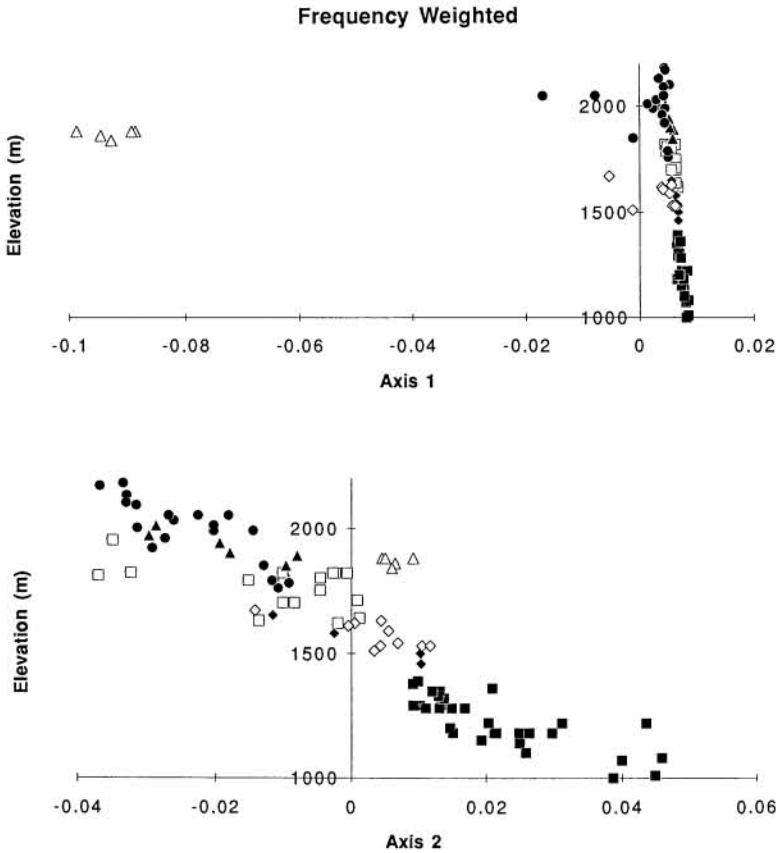

Figure 2. Relationship between axis 1 and elevation, and axis 2 and elevation for the West Usambara principal coordinates analysis with the chi-squared similarity coefficient weighted by species frequency. ■ Ambangulu. □ Baga. ◆ Gonja. ◇ Mkussu. ▲ Shagayu. △ Shume-*Juniperus*. ● Shume–Magamba.

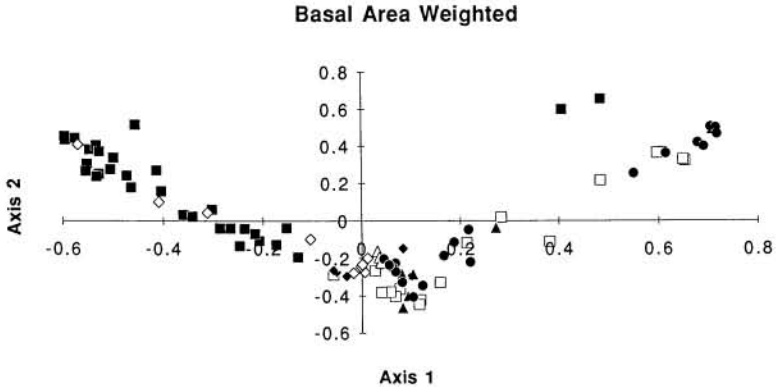

Figure 3. Relationship between axis 1 and axis 2 for the West Usambara principal coordinates analysis with chord distances weighted by basal area. ■ Ambangulu. □ Baga. ◆ Gonja. ◇ Mkussu. ▲ Shagayu. △ Shume-*Juniperus*. ● Shume–Magamba.

with high diversity were found throughout the elevational range, with the plot containing the highest number of species and the highest Shannon and lowest Simpson diversity value occurring at 1850 m. There was a positive correlation between stem density and elevation (Table 1).

In the Udzungwa mountains, as vegetation of lower elevation ridge tops was woodland and upper ridges were steep sided, there were more valley bottom and valley side plots at lower elevations, and more ridge-top plots at higher elevations. There was no obvious differentiation of ridge top, valley side or valley bottom plots in any of the ordinations, other than the difference in sampling intensities at different elevations. Plot elevation was correlated with axis 1 of the presence/absence and frequency-weighted ordinations. The ridge-top plot with the lowest axis 1 value in the frequency-weighted ordination had a markedly different structure to the other plots, with the highest stem density (704 ha^{-1}). Trees in the plot were also unusual, with species such as *Ternstroemia polypetala*, which has an unusual distribution, being apparently markedly disjunct between eastern and western Africa (White 1981, 1983b) and in the adjacent Uluguru mountains is restricted to narrow high elevation ridge tops (Pócs 1976b). There was no relationship between plot elevation and axis 1 value in the basal area-weighted ordination, but there was a correlation with the occurrence of large *Parinari excelsa* trees (Figure 4). The total basal area of *P. excelsa* in the Udzungwa plots was 127 m^2, or 37% of the total basal area measured. Plots with axis 1 values of less than −0.4 were dominated by *P. excelsa* which was virtually absent in plots (only one small tree) with axis 1 values of greater than 0.4. Thus, the group of plots with negative axis 1 values were dominated by *P. excelsa*, which occurred in ridge-top, valley bottom and valley side plots with an elevational range of 490–1580 m (Figure 4).

Stem density in the Udzungwa plots was positively correlated with elevation on ridge tops ($r^2 = 0.54$, $P = 0.0001$), valley sides ($r^2 = 0.32$, $P = 0.0009$), but

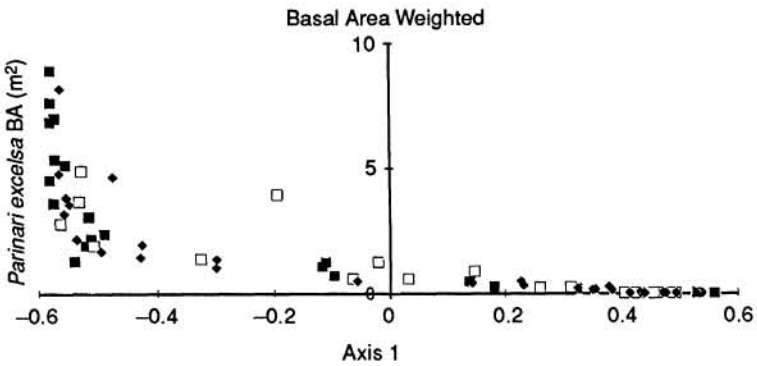

Figure 4. Relationship between axis 1 and basal area of *Parinari excelsa* in each plot for the Udzungwa principal coordinates analysis with chord distances weighted by basal area. ■ ridge-top plots, □ valley bottom plots, ◆ valley side plots.

not valley bottoms ($r^2 = 0.066$, $P = 0.24$). The stem density in ridge-top plots is significantly higher ($P < 0.01$) than that in both valley side and valley bottom plots. A similar correlation was found in the Nguru plots. Fifteen of the Nguru plots were on ridge tops, the remaining 14 were on valley sides. Stem density was significantly different between the Nguru ridge top and valley side plots ($P < 0.01$). Nguru plot diversity was not associated with ridge tops ($P > 0.05$) and there was a poor correlation between the higher Nguru stem densities and higher diversity. Basal area of the Udzungwa plots was positively correlated with elevation in valley bottom plots ($r^2 = 0.39$, $P = 0.0014$), valley side plots ($r^2 = 0.17$, $P = 0.023$) but not ridge-top plots ($r^2 = 0.08$, $P = 0.18$). However, this may have been related to a longer history of logging at lower elevations rather than being a true elevational trend.

Throughout the elevational range, ridge-top, valley bottom and valley side Udzungwa plots could be both rich in species and diverse. A number of plots of low diversity and high dominance occur at mid-elevations on ridge-top, valley bottom and valley side plots. Of the 10 plots with the highest Simpson's index, three valley bottom plots were dominated by *Cephalosphaera usambarensis* (62% of stems, mean Simpson's index = 0.41), three ridge-top plots and two valley side plots were dominated by *Parinari excelsa* (59% of stems, mean Simpson index = 0.38), one valley side plot was dominated by *Brachystegia microphylla* (70% of stems, Simpson's index = 0.51) and the least diverse ridge-top plot was dominated by *Trichoscypha ulugurensis* (85% of stems, Simpson's index = 0.72).

To compare forests at similar elevations at the three sites all the Nguru plots were included with subsets of the Udzungwa and West Usambara plots to create a set of mid-elevation plots. The Nguru data set is the smallest of the three available with an elevational range of 880–1560 m. The elevation range of the Udzungwa plots used was 800–1670 m and the West Usambara plots, 1000–1700 m. The 130 plots contained 2600 trees of 174 species with a total basal area of 653 m^2 and covered an estimated 12.9 ha. The relationship between axis 1 of the three ordinations used and elevation is shown in Figure 5. For all three sites, elevation was correlated with axis 1 of the presence/absence (Usambara $r^2 = 0.69$, Nguru $r^2 = 0.80$, Udzungwa $r^2 = 0.79$) and frequency-weighted (Usambara $r^2 = 0.49$, Nguru $r^2 = 0.83$, Udzungwa $r^2 = 0.54$) ordinations. Excluding the low-value axis 1 outlier of the frequency-weighted ordination from the data set and re-ordinating the plots increased the correlation (all plots $r^2 = 0.71$, Udzungwa $r^2 = 0.68$). The outlier was the high stem density distinctive ridge-top plot mentioned above. Axis 1 of the basal area-weighted ordination was not well correlated with elevation (Usambara $r^2 = 0.027$, $P = 0.25$, Nguru $r^2 = 0.055$, $P = 0.22$, Udzungwa $r^2 = 0.099$, $P = 0.026$). Low axis 1 values in this ordination were associated with presence of large *Parinari excelsa* trees.

For the presence/absence ordination, slopes of elevation against axis 1 were within the 95% confidence limits of each other for all three sites, though the

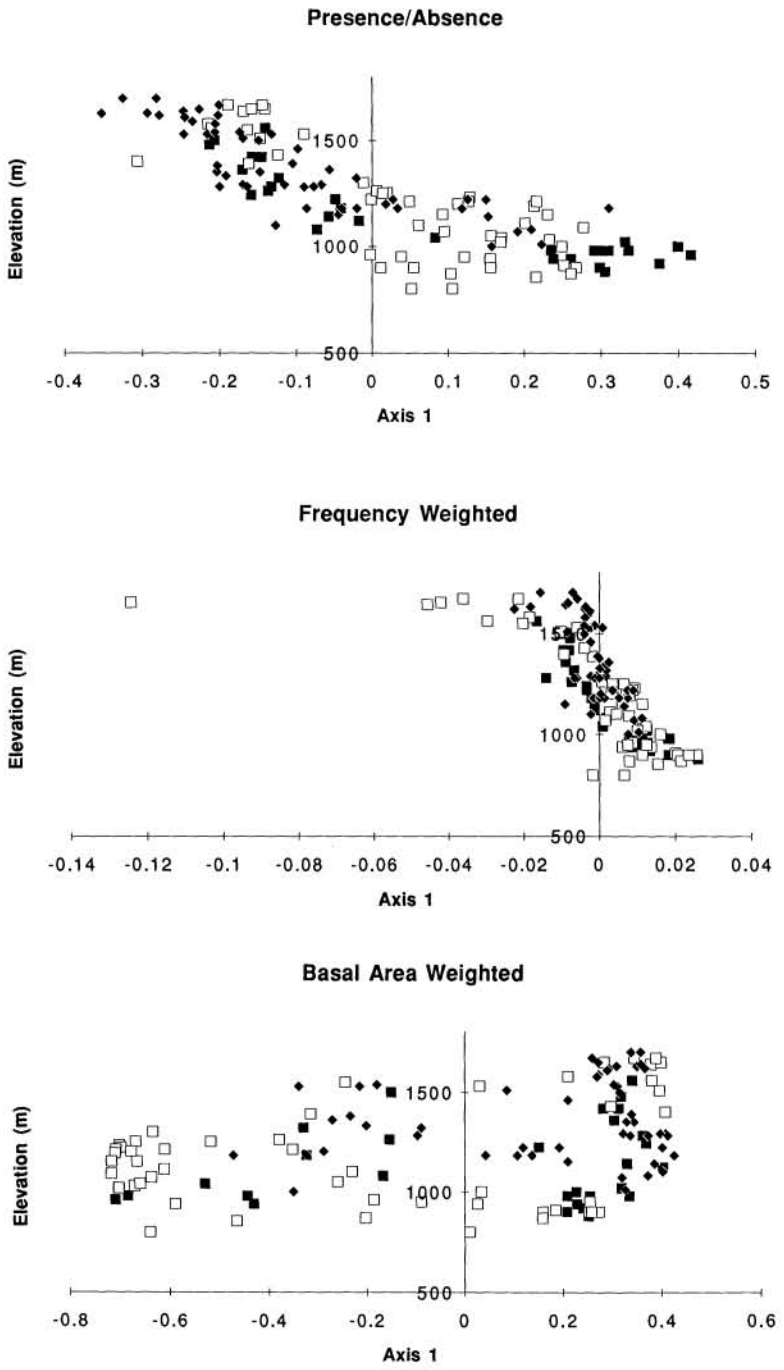

Figure 5. Relationship between axis 1 and plot elevation for the combined mid-elevation principal coordinates analysis with: Jaccard's similarity coefficient based on species presence/absence, chi-squared similarity coefficient weighted by species frequency and chord distance weighted by basal area. ■ Nguru mountains. □ Udzungwa mountains. ◆ West Usambara mountains.

Udzungwa slope was less than the other two (Usambara: $y = -1058x + 1266$; Nguru: $y = -813x + 1207$; Udzungwa: $y = -1330x + 1248$). For the frequency-weighted ordination, excluding the Udzungwa outlier, the Usambara and Nguru slopes were similar (Usambara: $y = -10{,}642x + 1252$; Nguru: $y = -13{,}532x + 1235$), but the Udzungwa slope was outside the 95% confidence limits of the other two sites ($y = -17{,}679x + 1295$). Axis 1 values of the basal area-weighted ordination of the Udzungwa plots were significantly different (by t-test) from the other two sites ($P < 0.01$), but the Nguru and Usambara plots were similar ($P > 0.05$).

DISCUSSION

The results are discussed in the context of elevational zonation, environmental discontinuities and dynamic processes. The good correlation between axis 1 and elevation of the ordination based on species presence/absence demonstrates that there is a steady replacement of species with elevation. This accords with results from the East Usambara mountains (Hamilton *et al.* 1989) and Uganda (Hamilton 1975). A vegetational continuum probably reflects an environmental continuum (Hamilton 1975) and there is no evidence of a critical altitude or zone at around 1500 m as has been suggested for north-east tropical Africa (Friis 1992), Mt Cameroon (Boughey 1955) or Malesia (van Steenis 1984). If floristic zones do exist, and they are not a product of sampling or method of analysis, then a possible reason for absence of a 1500 m zone in elevational distribution of West Usambara forest trees is that the elevational range of the plots analysed here does not cross a zone boundary. For example, the boundary between the Afromontane and Zanzibar–Inhambane regions of White (1983a) is at 1254 m in the East Usambara mountains and may be below the elevations sampled in the West Usambara. However, absence of a discontinuity in the Udzungwa plots, which have an elevation range of 450–1760 m suggests that zones based on species presence/absence cannot be recognized in the Eastern Arc forests.

Weighting the plot data with species frequency created discontinuities not seen with presence/absence data. This suggests that there are environmental discontinuities, and consequently zones could be recognized within the forests sampled. Ordination based on frequency separates the Shume-*Juniperus* forest from the other forest plots. The Shume-*Juniperus* plots were dominated by *Catha edulis*, which contributed 55% of the individuals and 45% of the basal area in the five plots sampled in that area, and was relatively rare in the other plots. The dominance of *Catha* is also reflected in low richness and high dominance values. Structurally, the Shume-*Juniperus* plots have a similar tree density to the other plots, but a low basal area. So should a zone be recognized that separates the Shume-*Juniperus* forest from the other forest types on the West Usambara mountains? The Shume-*Juniperus* forest is in the rain shadow of the Mlomboza ridge, and is in an area much drier than the forests to the east. Compared to

the wetter forests, the canopy is more broken with a higher grass cover in the herb layer. The avifauna is different from that of the Shume–Magamba forest (Lovett & Stuart, in press), and with genera such as *Olea*, *Juniperus* and *Ptaeroxylon*, the flora has northern and southern affinities to Mediterranean climate vegetation in contrast to the tropical nature of wetter forests at a similar altitude (Lovett 1993a). Alternatively, as the Shume-*Juniperus* forest is separated from the moist forests by cleared land (Lovett & Stuart, in press), but at one time it would have been continuous with the moist forests, its distinctiveness could reflect a loss of connecting forest types.

The strong correlation of changes in community associations to elevation could be caused by a number of factors. Rainfall in the lower elevation plots from Ambangulu is higher than in the upper elevation plots. In the Uluguru mountains of Tanzania which are also in the Eastern Arc, Pócs (1976a) observed that rainfall distribution itself was insufficient to explain the great diversity of vegetation types. Temperature drops rapidly with altitude in forested areas, with a lapse rate of about 0.6°C/100 m (Pócs 1976a) to 1.7°C/100 m (Moreau 1935). The relationship between temperature and rainfall is probably not simple, as there are large annual variations in both factors; for example, cold season frosts usually occur at elevations of greater than 2000 m, but frosts as low as 1500 m have been observed in the West Usambara (Moreau 1935). In addition, species frequency can reflect past events. For example, the low diversity Shume–Magamba plot is dominated by a pioneer species *Macaranga kilimandscharica* and is on an old pitsaw site, suggesting that low diversity in this moist forest plot is related to early successional stage following disturbance for timber extraction. The occurrence of large *Ocotea usambarensis* trees in two of the Ambangulu plots is also indicative of long-term forest dynamics. Contrary to many African forest tree species, a certain amount is known about the ecology of *Ocotea usambarensis* as it is a valuable timber (Kimariyo 1971, 1972; Willan 1965). Large *Ocotea* trees which are not regenerating have been noted in the East Usambara mountains (Hamilton & Macfadyen 1989), and the species has an unbalanced population structure at Mazumbai in the West Usambara (Hall 1990). It does not reproduce well by seed, but suckers freely and has growth rates of 1.2 m y^{-1} for the first 5 y in a well-tended arboretum (Willan 1965) with an annual height increment of 0.92 m over 24 y in Lushoto arboretum (Mugasha 1978), or 0.3–0.5 m y^{-1} in the West Usambara (Willan 1965). Attempts to regenerate *Ocotea* at Mufindi in the southern Udzungwa were not successful (E. Mdemu, pers. comm.). One possibility for the dominance of *Ocotea* in the two Ambangulu plots is that the large trees are relictual from a former climate that favoured establishment of *Ocotea*. As *Ocotea* coppices, then the trees could be much older than even their large size indicates. Climatic changes have been suggested for occurrence of non-reproducing populations of *Tilia cordata* in northern England (Pigott & Huntley 1978, 1981), though it is important to note that seasonal climatic patterns, not mean temperatures,

determine the latitudinal extent of *Tilia* (Pigott 1981). As *Ocotea* is predominately a montane forest tree, then its occurrence at relatively low elevations could indicate that at some point in the past the climate was cooler. Alternatively, the *Ocotea* could be a relict of an earlier successional stage related to disturbance rather than climatic change. *Ocotea* has been observed to be a pioneer forest tree in Ericaceous communities (Backéus 1982), the extent of which may be largely determined by fire resulting from human activities (Lovett 1993a). There is archaeological evidence of early Iron Age settlement in the West Usambara suggesting that the forests were being utilized for industrial purposes 1800 years ago (Schmidt 1989). Forest disturbance and subsequent long-term dynamic processes could also be related to storm damage (Reid 1991), or possibly to earthquakes. Successional changes following physical disturbance, rather than climatic fluctuations, would better fit the suggestion that the Eastern Arc has been climatically relatively stable for long periods (Lovett 1993e, Lovett & Friis, in press). If this is the case, then species normally associated with montane forest may be restricted to higher elevations because of competitive community dynamics, and not as a result of physical factors such as temperature. Areas which are subject to environmental perturbations are more likely to show more successional stages, which could be interpreted as vegetation zones even though they are not due to environmental discontinuities.

Diversity is not well correlated with elevation. In the West Usambara mountains, with the exception of the Shume-*Juniperus* plots, diversity is similar in the different locations. In the Udzungwa mountains, high diversity and species-rich plots are found on ridge tops, valley bottoms and valley sides; and diversity is similar in the West Usambara, Nguru and Udzungwa mountains. The Udzungwa and Nguru ridge-top plots have high stem densities. The Eastern Arc ridge-top forests fit descriptions of ridge-top forest elsewhere in the tropics, which are considered to have highly leached, acidic, nutrient-poor soils, with slow growing trees with hard dense wood (Whitmore 1984). If elevation and productivity can be equated and ridge-top forests are assumed to have low productivity, then if productivity and diversity are related, they would be expected to be less diverse than sheltered, fertile, valley bottoms. In both Udzungwa and Nguru plots, diversity remained high throughout the elevational and caternary range of the samples. Moreover, as stem density is higher in the upper elevation ridge-top plots, on an area basis they are substantially richer than the lower plots.

The results indicate that high diversity is normal in the Eastern Arc forests, and at the local scale diversity is not necessarily related to species composition, elevation or edaphic factors. This suggests that stochastic events may lead to an equilibrium of large tree species richness over long periods of time in the geologically and climatically stable Eastern Arc mountains. However, correlation of community associations with elevation demonstrates that these are not

random assemblages, but determined by environmental factors related to elevation. High stem densities on ridge tops also suggests environmental determinism. In the Far East, there are structural and florisitic similarities between lowland heath forest and upper montane forest which have been attributed to similar low soil nutrient status (Whitmore 1984), though drought and waterlogging have also been implicated in determining heath forest structure (Newbery 1991). Diversity in lowland Ghanaian forests increases with rainfall and is inversely correlated with soil nutrients (Hall & Swaine 1976). In addition to nutrient supply, light is considered to be a major resource, determining patterns of relative abundance in tropical forests (Newbery *et al.* 1992). Ridge tops are more exposed to light compared to valley bottoms, and this may permit higher stem densities and consequently greater species packing.

If high diversity is the normal situation, caused by an interaction of stochastic and environmental factors over time, then low diversity plots require explanation rather than species-rich plots. As previously discussed, low diversity plots on the West Usambara mountains are associated with low rainfall and disturbance. The low diversity ridge-top plot in the Udzungwa mountains dominated by *Trichoscypha ulugurensis* is almost certainly the result of past disturbance. The *T. ulugurensis* stand is of relatively low small diameter trees, and the species is normally a mid-storey rather than canopy tree. Dominance of *Parinari excelsa* in other low diversity plots may be related to climatic fluctuations. *P. excelsa* is widespread in tropical Africa with a wide elevational and habitat range (White 1976). At Mwanihana it dominates on drier mid- to low-elevation slopes, which in the monomodal rainfall pattern of the Udzungwa mountains, will be subject to greater seasonal water stress than either valley bottoms or the cool, misty, upper elevation slopes. Low diversity in this case appears to be related to the dominant species being favoured by having a broad environmental tolerance. This was suggested by Stevens (1992) as an explanation for decreasing diversity with elevation, but in this case climate fluctuations are more local than envisaged by Stevens and not correlated with elevation. The low diversity valley side plot dominated by *Brachystegia microphylla* is also correlated with seasonal water stress, as *B. microphylla* is normally a woodland tree and the plot was on an exposed cliff edge. Clumping in *B. microphylla* may also be related to ectomycorrhizal associations, a condition reported from other species in the genus and associated with monospecific stands (Connell & Lowman 1989, Högberg 1989, Malloch *et al.* 1980). Species-specific biology may also be the reason for low diversity valley bottom plots dominated by *Cephalosphaera usambarensis*, which is a monotypic genus reaching heights of over 60 m with large seeds and shade-tolerant seedlings restricted to mid-elevation Eastern Arc forests (Mugasha 1983).

In the combined mid-elevation ordinations, plots from all three mountains show a similar relationship between elevation, species presence/absence and frequency of species occurrence. There is no marked difference in regression of

axis 1 values against elevation for the species presence/absence ordination, but the Udzungwa plots show a different relationship to the Usambara and Nguru plots in the frequency-weighted ordination. There is a poor correlation between axis 1 values and elevation for the basal area-weighted ordination, and the difference between the Udzungwa plots and the other two sites is even more marked. The results suggest that elevation is more important than latitudinally determined differences in climate between the three sites for determining species presence, but latitude affects the relative proportions of species in the plots in terms of both frequency and basal area.

The 3° of latitude difference between the West Usambara and Udzungwa mountain sites is apparently insufficient to demonstrate the significant decline in diversity commonly associated with increasing latitude (Latham & Ricklefs 1993, Pianka 1966, Rhode 1992, Rosenzweig 1992, Stevens 1989; Terborgh 1973, 1985; Wright *et al.* 1993). There are, however, differences in quantitative community associations related to the marked climatic difference. Non-biotic latitudinal changes are not linear, the temperature gradient has little variation between 20° North and South with climatic symmetry prevailing across the equator (Terborgh 1973). However, in tropical lowland forests, latitudinal decrease in species richness is asymmetrical about the equator with the southern decrease beginning near the tropic of Capricorn (23° 17′ S) and the northern decrease beginning at around 12° N (Gentry 1988). In eastern tropical Africa, forests north of the equator are markedly less diverse than forests south of the equator. For example, there are *c.* 260 species of tree greater than 8 m tall in the forests of north-east tropical Africa (Friis 1992, 1993) compared to more than 600 forest tree species greater than 10 m tall in Tanzania (Lovett, unpublished data). Rainfall patterns show a climatic asymmetry around the equator; for example, in the mean of relative range in accumulated annual rainfall (annual maximum − annual minimum divided by mean annual rainfall; Stevens 1989). In the Neotropics diversity increases linearly with precipitation (Gentry 1982) but seasonality is also important, with forests in more seasonal climates being less diverse than those in which rainfall was evenly distributed throughout the year (Gentry 1988). In the Eastern Arc, differences in seasonality apparently changes quantitative community associations, but not qualitative associations and diversity. This suggests that species composition and diversity is related to a long-term environmental history rather than seasonality *per se*, whereas other quantitative parameters are determined by short-term climatic factors.

In conclusion, similarity between forest tree plots in the Eastern Arc mountains appear to be determined by a number of factors. An elevational continuum as revealed by ordination based on species presence/absence shows there is a replacement of species with change in elevation, as would be expected with a simple gradient model. However, ordinations weighted by frequency demonstrate that rainfall can markedly affect species abundance and rapid changes in precipitation can give rise to apparent zonation. Weighting an ordination by

basal area provided evidence for long-term dynamics in the West Usambara forests, indicating that species presence or absence in a community may be related to past environmental events. Forest classification using zones or divisions of a continuum based on analysis of community associations thus needs to be interpreted in the light of possible historical events, as well as present physical conditions. Both random and deterministic processes appear to be involved in determining diversity as concluded by Gentry (1988). However, productivity does not appear to be obviously linked with local scale diversity patterns. High diversity can be considered as normal, and due to a build-up of species in a stable environment through stochastic processes within the limits of their tolerances. Low diversity is due to early successional stage, low rainfall, a locally fluctuating climate favouring taxa with broad tolerances or species-specific biological adaptations.

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